

SPECIES POOLS IN EASTERN ASIA AND NORTH AMERICA

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ABSTRACT

A species pool refers to the total species in a defined region at a given time. The species pool in eastern Asia is the product of a long history with low speciation rates, while the species pool in northwestern North America is largely due to recent rapid speciation. Data fail to support the theoretical dominance of ecological determinism in the development of regional species diversity. A species pool is the product of evolution, immigration, and extinction and thus postulates extant species richness to be an historical artifact rather than an ecologically determinate reality.

RESUMEN

La gran riqueza de especies en el este de Asia es el efecto de una historia larga con unas tasas de extinción y especiación bajas, mientras que la gran riqueza en el noroeste de Norte América es debida a especiación reciente rápida. Los datos no explican la dominancia teórica del determinismo ecológico en favor de la historia geofísica regional específica como base para explicar la diversidad regional de especies. Se propone un "pool" de especies como resultado de la evolución, inmigración y extinción, y por ello se postula que la riqueza en especies vivientes es un artefacto histórico en vez de una realidad ecológicamente determinada.

INTRODUCTION

Species diversity is a central theme of environmental studies. Scientists have accumulated much data on species diversity over the past 250 years. However, there are still no answers to some basic questions. One critical question that is frequently asked by scientists is why there are just so many species in a region, and not more or less than that number. In other words, what factors determine regional species richness? In fact, a comprehensive, rigorous, and general theory of species diversity is lacking (Solbrig 1991). Ricklefs (1987) thus claimed that species diversity is "the major, unexplained pattern in natural history," one that "mocks our ignorance."

One dominant hypothesis is that available energy determines regional species richness (Hairston et al. 1960, MacArthur and Wilson 1967, Currie and Paquin 1987, Moore 1987, Adams and Woodward 1989, Andersson 1990, Currie 1991). Currie and Paquin (1987) and Currie (1991) clearly claimed that

regional tree species richness can be explained in terms of actual evapotranspiration (AET). Alternatively, White (1983) claims that the tree species diversity pattern of the Northern Hemisphere is the product of extinction. Goldsmith (1985) believed that periodic, or episodic, catastrophic destruction of life was caused by comet or asteroid impacts. However, there are three critical problems with these positions: First, almost all studies of species richness concentrate, very naturally, on just one taxonomic group (e.g. pines, oaks) (Moore 1987). But each group may have some peculiar requirement of its own that obscures the general causes of species diversity (Moore 1987). Second, studies were often made using small biogeographic regions. Micro-environmental variations greatly influence the result when comparing two small regions. Third, more importantly, the conceptual definition of a species has not been consistent from taxonomist to taxonomist nor from region to region.

To minimize the observation biases caused by the factors mentioned above, this study examined all seed plants in the larger biogeographic regions in the Northern Hemisphere. Eastern Asia in this study refers to the eastern forest region of China, Far East and eastern Siberia of Russia, and Korea (Fig. 1). North America includes the continental regions of Canada and United States. The forests of North America are naturally divided into those west and those east of the Great Plains (Fig. 2). The boundary of the boreal zone in the Northern Hemisphere follows Larsen (1980) with modification in eastern Asia. The boreal region in Europe includes the area westward from the Ural Mountains (Fig. 3: I). Boreal eastern Asia includes eastern Siberia in Russia and the Da Xingan Ling Mountains of China (Fig. 3: II). The east-west division of the boreal zone in North America follows Daubenmire (1978). The eastern section includes the area east of the Rocky Mountains (100°W) (Fig. 3: IV) and the western or Cordilleran Section extends westward (Fig. 3: III).

In eastern Asia, the temperate forest region includes the Xiao Xingan Ling, Wanda, and Changbai mountains in Northeast China, southern portion of Far East of Russia, and northern Korea (Fig. 3: V). This region is known as the Korean pine conifer and hardwood forest region (Chou and Li 1990). In western North America, the temperate forest region covers portions or all of the Pacific Northwest states of Oregon, Montana, Idaho, Washington, and southern British Columbia (Fig. 3: VI). This region includes the Pacific Northwest forests (Franklin 1988) and the northern portion of the forests of the Rocky Mountains (Peet 1988). In eastern North America, the temperate forest region extends from northern Minnesota upper Great Lakes region and eastward to southern Canada and New England, including, toward the southeast, much of the Appalachian Plateau in New York and northern Pennsylvania (Braun 1967, Fig. 3: VII). The region is known as the Hemlock-white pine-Northern Hardwoods region (Braun 1967, Vankat 1979) as well as the mixed conifer and deciduous forest region (Bailey 1976).

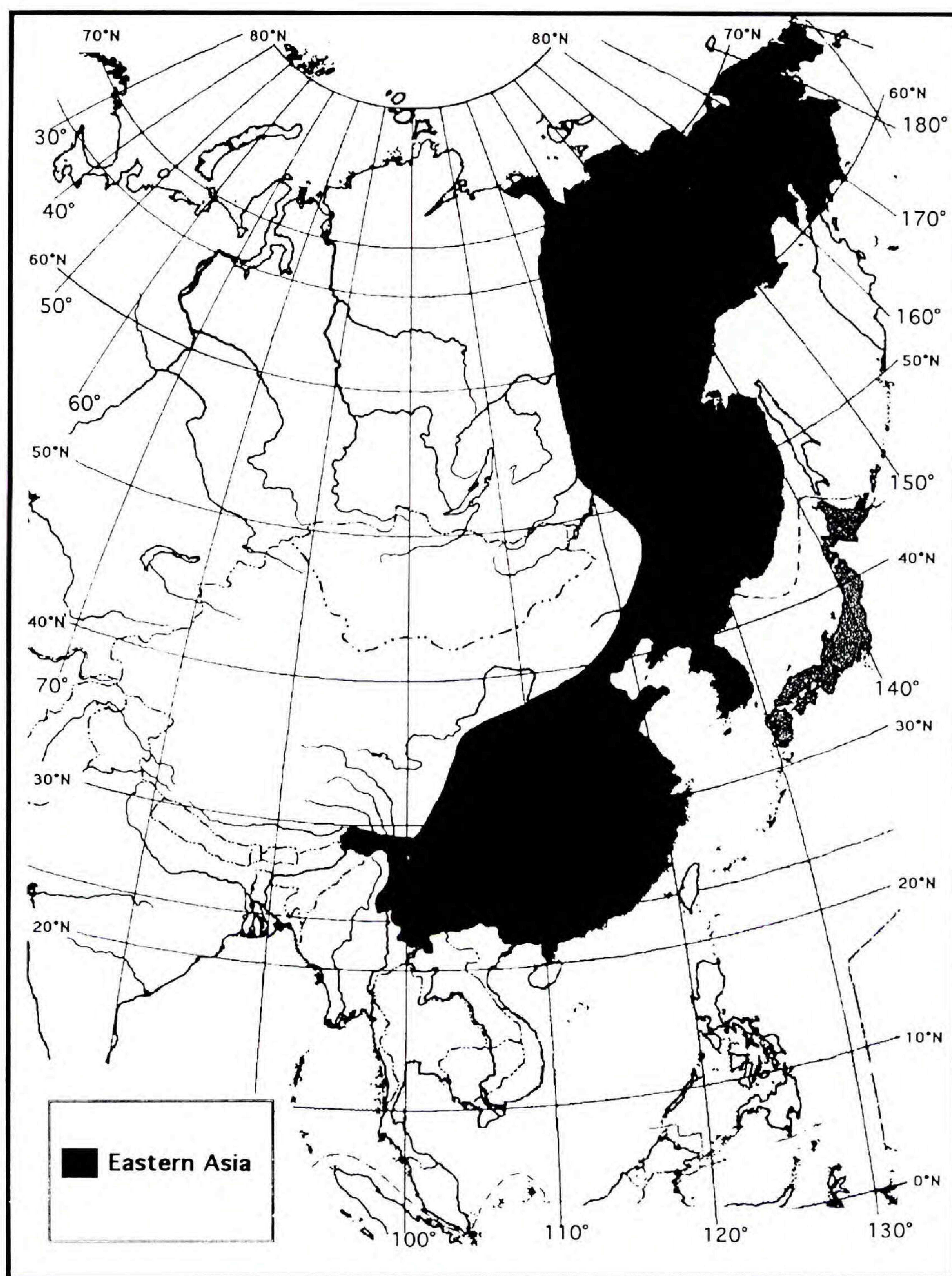


FIG. 1. Map showing the definition of eastern Asia in this study.

The main data sources of this study include field investigations, specimen observations, personal communications, and literature (including flora and fossil records). The primary data for eastern Asia were collected from a comprehensive forest survey conducted by authors and their colleagues at Northeast Forestry University and numerous forestry agencies during 1984-1988. Data for

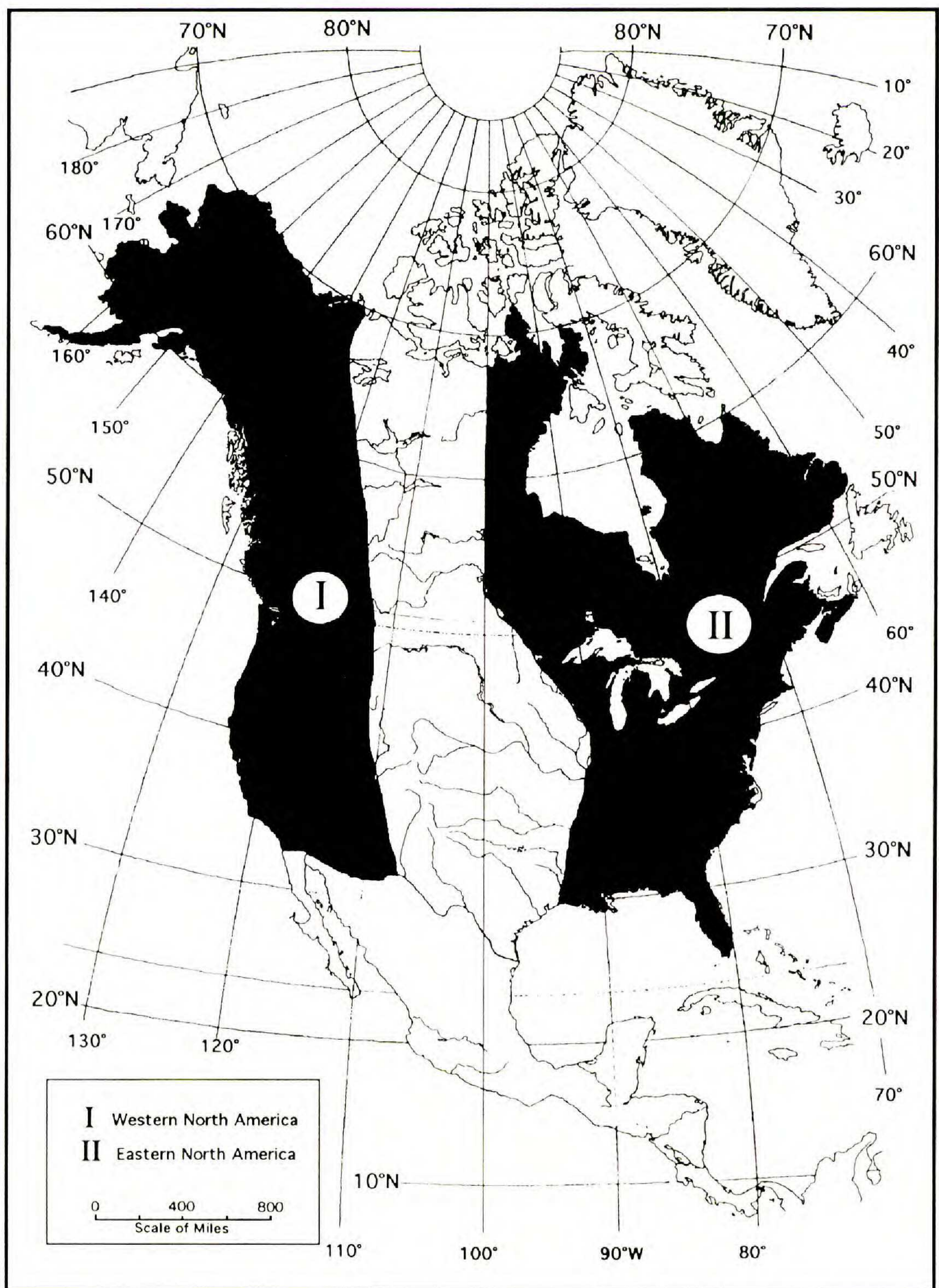


FIG. 2. Map showing the definition of western and eastern North America in this study.

North America is based on literature, supported where possible, by field collections, herbarium investigations, and personal interviews during 1989-1992. By using established methods and the same principal observer in the herbarium and field, the observational biases that often plague broad-scale comparisons were minimized.

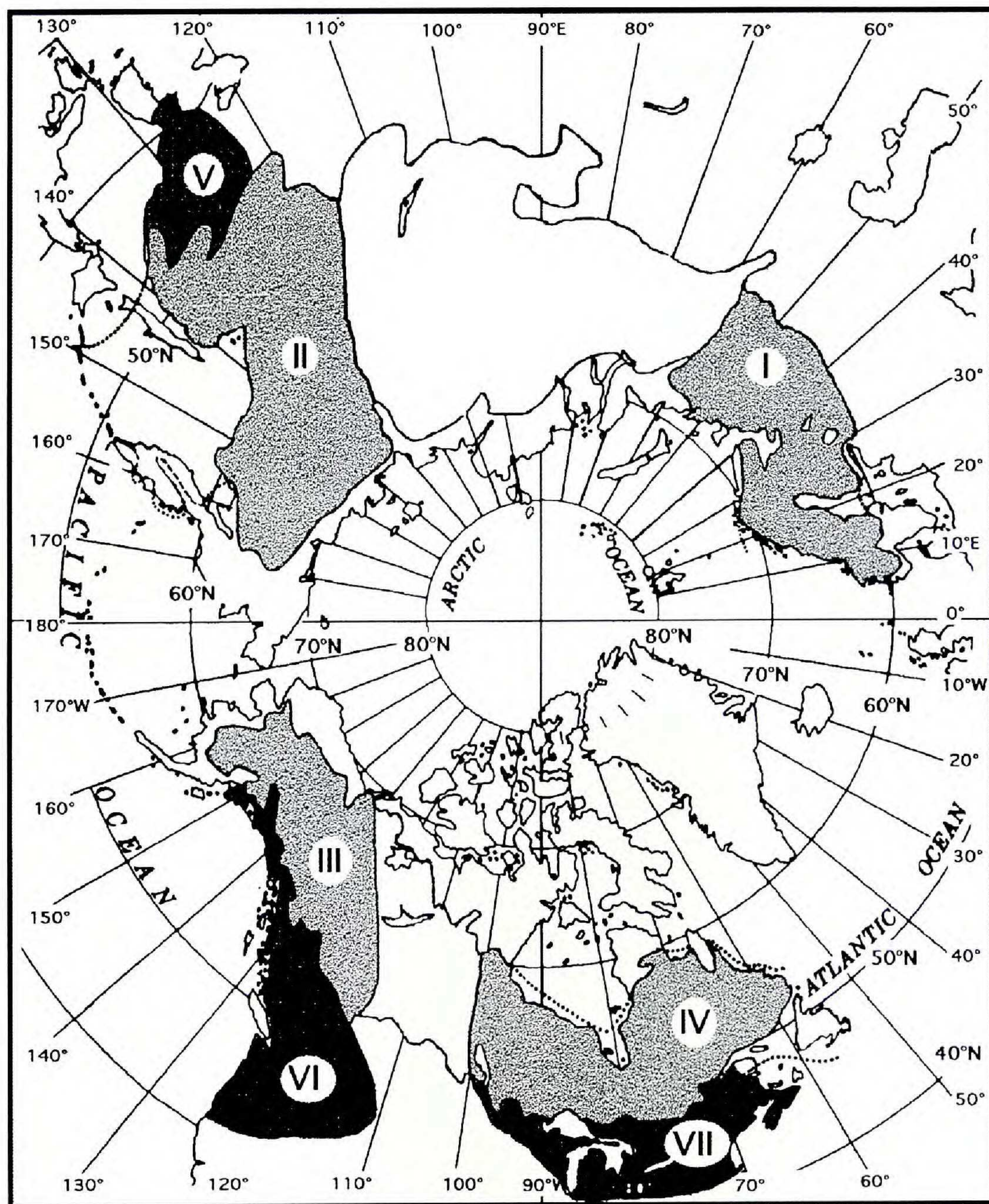


FIG. 3. Map showing the boreal and temperate forest regions involved in this study (I–IV—boreal forest zone: I–Europe, II–eastern Asia, III–western North America, IV–eastern North America; V–VII—temperate forest zone: V–eastern Asia, VI–western North America, VII—

Five sheets of voucher specimens of each taxon of seed plants found in the boreal and temperate forests of eastern Asia were collected during the field investigations. The location, life history, growth forms, function of woody plants, vegetative organs, habitats, and other characteristics such as flower color of each species were recorded for each specimen. The voucher specimens were retained in the Institute of Plant Sciences at Northeast Forestry University in Harbin, China. Manuals involving the floras of East Siberia, Far East, Korea, and Japan were also

used to identify voucher specimens. Herbarium collections, located in Northeast Forestry University, the Botanical Institute in Beijing, and the Applied Ecological Institute in Shenyang were also used to confirm identification of voucher specimens. Seed plant checklists of the boreal and temperate forests of eastern Asia were created separately from these comparisons. Additional floristic checklists were created separately for boreal Europe, boreal western North America, boreal eastern North America, temperate Japan, temperate western North America, and temperate eastern North America using scientific references: Ohwi (1965), Polunin (1959), Gleason and Cronquist (1991), Hitchcock and Cronquist (1974), and Scoggan (1978–1979).

In both boreal and temperate forest comparisons of Europe, eastern Asia, and western and eastern North America, floristic analyses were made at the family, genus, and species levels. Evolutionary analyses of flora were based on the diversification ratios (family and genus size), diversification rate (Eriksson and Bremer 1992), and flower characters. Phylogenetic analyses were made in terms of three categories: 1) primitive—subclasses Magnoliidae and Alismatidae; 2) intermediate—subclasses Caryophyllidae, Hamamelidae, Dilleniidae, Rosidae, Arecidae, Commelinidae, and Zingiberidae; and 3) advanced—subclasses Asteridae and Liliidae (following Cronquist's system in 1988).

EASTERN ASIA: A LONG EVOLUTIONARY HISTORY COUPLED WITH LOW SPECIATION RATES

The great plant species diversity of eastern Asia is well-known and has been widely emphasized by scientists (Sargent 1913, Hu 1935, Takhtajan 1969, Li 1952, Wu and Wang 1983, Boufford and Spongberg 1983, Latham and Ricklefs 1992). To date, 25,480 species of native vascular plants have been identified in eastern Asia, representing 300 families and 2,875 genera (Li 1993). This amounts to 10.7% of the total known species in the world and about 1.6 times the figure for North America (Table 1). The great plant diversity in eastern Asia is the product of long evolutionary history. The geological and paleobotanical records failed to support the existence of continental Quaternary glaciers in most of eastern Asia and thus extinction is not a main process in the development of the extant eastern Asian flora. Also, eastern Asian flora consists of a host of taxa that are presumed to be phylogenetically primitive, with many occurring as monotypic taxa in the subtropical or tropical regions. These factors have led to the concept that eastern Asia was the evolutionary source of modern flora in the Northern Hemisphere (Takhtajan 1969, Latham and Ricklefs 1992).

Ferns are phylogenetically primitive vascular plants. 52 families (80.0% of the total flora of the world), 204 genera (46.0%), and 2,300 species (19.5%) of ferns are known in eastern Asia. The family, genus, and species numbers are 3.5, 3.4, and 6.7 times those in North America, respectively. Gymnosperms, another phylogenetically primitive group of plants, are represented by ten families

TABLE 1. Comparison of taxon richness of native vascular plants of eastern Asia and North America.

	Eastern Asia *	North America **	World ***
Family			
Ferns	52	15	65
Gymnosperms	10	5	11
Angiosperms	238	202	542
Total	300	222	620
Genus			
Ferns	204	60	443
Gymnosperms	34	19	57
Angiosperms	2637	2261	12500
Total	2875	2340	13000
Species			
Ferns	2300	341	11820
Gymnosperms	180	118	670
Angiosperms	23000	15827	225000
Total	25480	16285	237490

Notes: * from Li (unpublished, 1988); ** based on Checklist of D. E. Moerman (Nancy Morin, pers. comm.); *** from Wu and Wang (1983).

in eastern Asia, but only five in North America. Eastern Asia contains almost all primitive monotypic families, including Ginkgoaceae, Cycadaceae, and Gneta-ceae. *Ginkgo*, for example, is the oldest of all trees, it dates back to the Triassic some 200 million years ago (Flora of North America Editorial Committee 1993). It is now naturally restricted to China although it was quite widespread in the world during the Cretaceous (Hsu 1983). Conifers apparently represent the greatest taxonomic diversity in eastern Asia. They are distributed among Eu-rope, eastern Asia, and western and eastern North America, respectively, ap-proximately in the ratio 1.0 : 3.4 : 2.1 : 1.6 by genus and 1.0 : 5.9 : 2.4 : 1.2 by species (Table 2).

There are 2,637 genera and 23,000 species of angiosperms belonging to 238 families native to eastern Asia (Li 1993). The family, genus, and species num-bers in eastern Asia are 1.4, 1.2, and 1.6 times those in North America, respec-tively. Almost all ancestral families of angiosperms based on fossil records have greater diversities in eastern Asia than in North America. Chloranthaceae, as the earliest angiosperm (appeared in the early Cretaceous, Muller 1981) has three genera and 16 species in eastern Asia and only one genus and one species in North America. Aquifoliaceae, one of the earliest woody angiosperm families (Muller 1981) represents 168 species in eastern Asia and about 20 species in North America. Moreover, Magnoliaceae, the most phylogenetically primitive woody family of angiosperms (Hutchinson 1973), contains 12 genera and 250 species ranging from Asia to North America (Wu and Wang 1983). Ten genera and 100 species of this family are known in eastern Asia, but only two genera

TABLE 2. Distribution of conifer species among Europe, eastern Asia, and western and eastern North America.

Family/genus	Europe	Eastern Asia	Western North America	Eastern North America
Cephalotaxaceae				
<i>Cephalotaxus</i>	0	7	0	0
Taxaceae				
<i>Amentotaxus</i>	0	4	0	0
<i>Pseudotaxus</i>	0	1	0	0
<i>Taxus</i>	1	6	1	2
<i>Torreya</i>	0	3	1	1
Taxodiaceae				
<i>Cryptomeria</i>	0	1	0	0
<i>Cunninghamia</i>	0	2	0	0
<i>Glyptostrobus</i>	0	1	0	0
<i>Metasequoia</i>	0	1	0	0
<i>Sciadopitys</i>	0	0	0	0
<i>Sequoia</i>	0	0	1	0
<i>Sequoiadendron</i>	0	0	1	0
<i>Taiwania</i>	0	2	0	0
<i>Taxodium</i>	0	0	0	2
Cupressaceae				
<i>Chamaecyparis</i>	0	1	2	2
<i>Calocedrus</i>	0	2	1	0
<i>Cupressus</i>	0	7	12	0
<i>Juniperus</i>	6	19	5	5
<i>Thuja</i>	0	2	1	1
<i>Thujopsis</i>	0	0	0	0
Pinaceae				
<i>Abies</i>	5	22	7	2
<i>Cathaya</i>	0	1	0	0
<i>Cedrus</i>	1	0	0	0
<i>Keteleeria</i>	0	9	0	0
<i>Larix</i>	1	10	2	1
<i>Picea</i>	3	16	6	1
<i>Pinus</i>	9	23	19	13
<i>Pseudolarix</i>	0	1	0	0
<i>Pseudotsuga</i>	0	6	2	0
<i>Tsuga</i>	0	6	3	3
Total Genera	7	24	15	11
Total Species	26	153	63	32

and 9 species are known in North America. Hamamelidaceae, another primitive family, has 25 genera and 90 species widely distributed in eastern and southeastern Asia and North America with some reaching south to Australia and Africa. 17 or 18 genera and 70 species of this family are known in eastern Asia. *Disanthus*, *Exbucklandia*, and *Rhodoleia*, ancestral genera of

the family (Takhtajan 1969), are all found in southern China. Only three genera and five species are present in North America.

The data above imply that eastern Asian flora has a long evolutionary history. However, the analysis of diversification rates (Eriksson and Bremer 1992) of families based on fossil records shows that species diversification rates* of most families in eastern Asia are much lower than those in North America. 20.7% of the total species in eastern Asia belong to families with low diversification rates ($R < 0.15 \text{ my}^{-1}$), while only 11.2% of the total species in North America belong to the same families.

Thus, we concluded that the great taxonomic richness of eastern Asia is largely the result of a lengthy evolutive history coupled with low extinction and low diversification rates.

NORTHWESTERN NORTH AMERICA: A SHORT EVOLUTIONARY HISTORY COUPLED WITH HIGH SPECIATION RATES

Geologically, northwestern North America is young. But the northwestern North American flora has the highest species diversity among all northerly regions in the Northern Hemisphere (Table 3 and 4). This great species diversity results from high speciation in a short evolutionary history.

The taxonomic and evolutionary structure of extant flora is consistent with the concept of a geologically young western North America. In the temperate zone, for example, western North America has a total 3,161 species, which is about 50% of the total species of all three temperate floras and about 1.5 times that of either eastern Asia or eastern North America. However, this flora has 19 families fewer than in eastern Asia and 27 families fewer than in eastern North America (Li 1993). Therefore, families of temperate floras, on average, have more species in western North America (roughly 30 species per family) than in eastern Asia (roughly 17) and eastern North America (15, see Table 5). Theoretically, the larger the family (containing more species), the more evolved (Stebbins 1981), because family is parental to species. From this point of view, the temperate flora in western North America is young.

The evolutionary analysis of flowers strengthens this statement. The solitary flower, both terminal and axillary, is the initial form of arrangement for flowers, while inflorescence is more advanced and of a greater biological advantage (Takhtajan 1991). In the temperate zone, western North America contains the highest proportion of inflorescence (87.8% of the entire flora, compared with 80.4% in eastern Asia and 79.1% in eastern North America) (Li 1993). Flower color is an important factor affecting pollination of plants. Green flowers are

*Diversification rate (R) refers to the speciation rate minus the extinction rate and is measured as the number of extant species over the time since the first appearance of a family. R is measured by the species number per million years (my^{-1}).

TABLE 3. Family, genus, and species richness of the seed plants in the three temperate regions.

	Eastern Asia	Western North America	Eastern North America	Total
Family				
Total	125	106	133	144
Genus				
Trees	30	23	43	52
Shrubs	74	54	77	119
Lianas	10	2	5	13
Herbs	537	574	495	909
Total	652	650	615	1090
Species				
Trees	65	50	95	200
Shrubs	228	235	263	652
Lianas	13	9	10	31
Herbs	1786	2867	1632	5505
Total	2092	3161	2000	6388

TABLE 4. Family, genus, and species richness of the seed plants in the four boreal regions.

	Europe	Eastern Asia	Western North America	Eastern North America	Total
Family					
Total	84	95	76	80	104
Genus					
Trees	18	20	14	20	25
Shrubs	35	44	37	46	59
Lianas	0	5	0	1	5
Herbs	215	311	278	206	385
Total	266	379	326	268	470
Species					
Trees	25	36	28	45	117
Shrubs	84	113	127	100	279
Lianas	0	6	0	1	7
Herbs	597	1006	1012	612	1970
Total	706	1161	1167	758	2373

largely pollinated by wind, and thus the anemophilous plants are claimed to be primitive in evolution (Takhtajan 1991). Alternatively, bright colored flowers are usually pollinated by insects, and entomophilous plants are considered more advanced in evolution. In western North America, only 21.8% of the total species have green flowers, a lower percentage than in either eastern Asia (27.8%) or eastern North America (33.6%). However, colorful flowers (white, yellow, pink, rose, purple, blue, and red) are more frequent in western North America

TABLE 5. Comparisons of evolutionary levels of the temperate and boreal floras based on the ratios of genera/family, species/family, and species/genus.

	Europe	Eastern Asia	Western North America	Eastern North America
Genus No./Family				
Temperate		5.2	5.3	4.6
Boreal	3.2	4.0	4.3	3.4
Species No./Family				
Temperate		16.7	29.8	15.0
Boreal	8.4	12.2	15.4	9.5
Species No./Genus				
Temperate Zone				
Trees		2.2	2.2	2.2
Shrubs		3.1	4.3	3.4
Lianas		1.3	4.5	2.0
Herbs		3.3	5.0	3.3
Total		3.2	4.9	3.3
Boreal Zone				
Trees	1.4	1.8	2.0	2.3
Shrubs	2.4	2.6	3.4	2.2
Lianas	0.0	1.2	0.0	1.0
Herbs	2.8	3.2	3.6	3.0
Total	2.7	3.1	3.6	2.8

and comprise 78.2% of the total flora. The same colors account for 72.2% in eastern Asia and 66.4% in eastern North America.

Life history, as the result of natural selection, reflects the long-term adaptation of a plant to its environment. Annuals are unknown in primitive ferns and gymnosperms, but their sexual reproduction processes enable them to persist in habitats that restrict the establishment of perennials. Therefore, annuals are believed to arise relatively late in the evolution of terrestrial plants (Bazzas and Morse 1991). Annuals are distributed among eastern Asia, western and eastern North America at the ratio of 1.0 : 2.5 : 1.0. Alternatively, as the early evolved group, trees are distributed among eastern Asia, western and eastern North America at ratios based on total numbers of both genus and species as follows: 1.3 : 1.0 : 1.9. Obviously, the temperate flora in western North America is relatively young in evolution relative to the other two temperate floras.

Further, phylogenetic data strengthen the argument. Magnoliidae and Alismatidae are the most primitive taxa of flowering plants in Cronquist's system (1988). They, together with gymnosperms represent the lowest diversity in temperate western North America (16 families and 56 genera) and the highest in temperate eastern Asia (23 families and 72 genera). But Asteridae and Liliidae, the most advanced taxa in Cronquist's system have the highest diversities in tem-

perate western North America (243 genera, compared with 233 genera in temperate eastern Asia and 199 in temperate eastern North America respectively).

In brief, all these evidences from taxonomic structure of flora, flower diversity, life history and phylogeny show that northwestern North American flora is relatively young in evolution. However, data on diversification rates (R) for families show that there is high species diversification in northwestern North America. A total of 25 families with low diversification rates ($R < 0.10 \text{ my}^{-1}$) are recorded in the temperate regions, and they are distributed among eastern Asia, western and eastern North America, respectively, at a species ratio of 2 : 1 : 3 (Table 6). Western North America clearly has the smallest taxon diversity among families with low diversification rates. In contrast, the nine families with higher diversification rates ($R > 0.60 \text{ my}^{-1}$) are distributed at a ratio of total number of species of 1 : 3 : 1 in eastern Asia, western and eastern North America. Further, three genera with the highest diversification rates, *Astragalus*, *Senecio*, and *Carex* display maximum species richness in western North America and exceed that of any other region (279 species relative to 51-145 species in the temperate regions and 144 species relative to 56-90 species in the boreal regions). Boreal floras show a similar pattern (Li 1993).

Thus, there is little doubt that the data indicate that the northwestern North American flora is the product of high species diversification and relatively recent evolution. Considering that the species-rich northerly flora of western North America has over 50% of the total species restricted to this region, we conclude that this great species richness in northwestern North America is largely the effect of rapid speciation rather than immigration.

SPECIES POOL HYPOTHESIS

Based on our studies, we argue that species exist in a pool in a given region at a given time. This regional species pool is a relatively static spot in a dynamic river of species diversity development over time. It is the result of two additive processes: speciation and immigration; and, one subtractive process: extinction (both locally and globally) (Fig. 4, Table 7)! Thus, a species pool has largely an historical rather than an ecological basis for its existence (Li 1993).

Speciation is the formation of new species from pre-existing ones usually by a process of improved adaptation of survivors to the environment. New species may be better adapted to the environment and replace the less well adapted ones. Speciation began long ago and is still going on. It is best characterized as a regional subset of the global genetic pool. The rate of speciation depends not only on environmental diversity within the pool, especially under conditions of geographic or ecological isolation, but also on chance. Thus, it is impossible to predict the speciation rate for a region.

Immigration, however, does not involve global genetic variability, but does

TABLE 6. Evolutionary levels of temperate and boreal floras based on diversification rates (R).

Diversificate Rate (R)	Europe	Eastern Asia	Western North America	Eastern North America
$R < 0.10 \text{ my}^{-1}$*				
Temperate				
Family Number		21	11	22
Species Number		77	42	111
% of Total Species		3.7	1.3	5.6
Boreal				
Family Number	10	13	7	11
Species Number	21	35	7	11
% of Total Species	3.0	3.0	1.7	4.6
$R > 0.60 \text{ my}^{-1}$*				
Temperate				
Family Number		8	9	9
Species Number		95	258	91
% of Total Species		4.5	8.2	4.6
Boreal				
Family Number	6	8	7	6
Species Number	45	83	108	42
% of Total Species	6.4	7.1	9.3	5.5

Notes: *species per million years.

TABLE 7. Basic patterns of development of regional species pool.

Environmental Pattern								
Historical Changes	+	+	+	+	-	-	-	-
Heterogeneity in Pool	+	+	-	-	+	+	-	-
Barriers around Pool	-	+	-	+	-	+	-	+
Process								
Extinction	+	+	+	+	-	-	-	-
Speciation	+	+	-	-	+	+	-	-
Immigration	+	-	+	-	+	-	+	-
Species Diversity	M	M [@]	L	L	H	H [@]	L	L
Example	CI	NW	NE	EE	X	SEA	NEA	SP

Notes: “+” represents great and “-” represents weak; L—low, M—median, H—high; @ represents more endemic species. CI—some continental islands; NW—northerly western North America; NE—northerly eastern North America; EE—extreme environment; X—unidentified region; SEA—southerly eastern Asia; NEA—northerly eastern Asia; SP—specialized habitat.

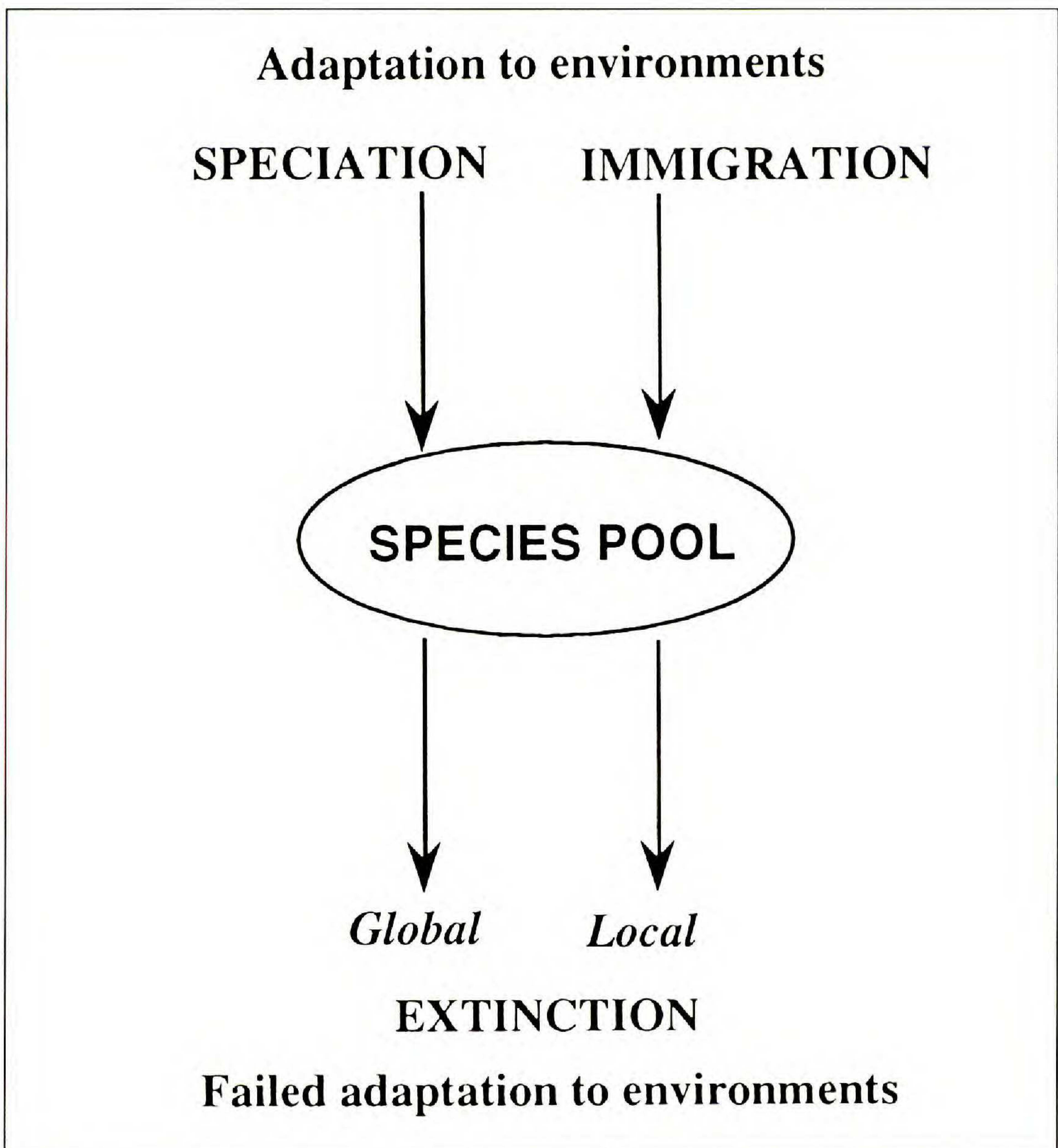


FIG. 4. Species pool in a given region at a given time (After Li 1993).

contribute to regional changes. During migration, species may evolve. If genetic change makes it possible to distinguish new species from the parent species, this process is evolutionary (speciation); if not, it is called immigration. Both natural selection and chance play roles in immigration of species to a region. This also means that the absence of a species in a region may result purely from chance rather than deterministic natural processes.

Extinction of a species can occur locally (exclusion or emigration), in which one or more populations vanish but others survive elsewhere, or globally, in which all members of the species population everywhere in the world vanish. Extinction of a species is a natural process. The fossil record indicates that most, if not all, species have a finite life span, averaging between 1 and 10 million

years (Solbrig 1991). Drastic environmental change is a major cause of species extinction especially on a global scale. Because the environment is in a constant state of transformation, some species are always being lost while others are added. Some changes in the physical environment are cyclic and periodical, while others are less predictable. Thus, it is impossible to establish a normal rate of species change and based on the data presented in this study, it may be impossible to do so at all.

A species pool has the following main characteristics.

Liquidity and Irreversibility

A species pool is a dynamic flow of species through a storage area. Adapted to new environments, species that have become locally extinct (exclusion) may re-migrate back into a region. However, the natural process from speciation to extinction is irreversible. Species that have become globally extinct cannot be recovered naturally. Thus, conservation of biodiversity is needed on a global level. But, it is impossible for humans to interrupt the natural extinction process and store all species on a global scale. Man can temporarily store as many species as possible in regional species pools, but even these are present only on a dynamic basis.

A species pool is not the accumulation of species only over long evolutionary time spans, and species-rich communities may not always be the oldest as Whittaker (1977) has stated. Western North America has a young geological history. The rapid rise of the Rocky Mountains in the Tertiary and extensive glaciation in the Pleistocene caused widespread extinction of life in western North America. However, western North America has the greatest species pool in the northerly regions of the Northern Hemisphere. The northerly flora of western North America, which is both young and species-rich, is a striking example that fails to support Whittaker's hypothesis. This fact is also not consistent with White's hypothesis that emphasizes that the differences in taxon richness among eastern Asia, North America, and Europe results from differing Pleistocene extinction rates in the three areas (White 1983). In fact, it is not realistic to focus on preservation of static ecosystems for preservation of maximum species richness or biodiversity.

Stochasticity and Non-equilibrium

Nature is not in balance. Disturbances and irregularities of all sorts are not aberrations, but integral parts of nature (Solbrig 1991). Both chance and natural selection produce the steady coming and going of species through a pool. Speciation, immigration, and extinction function continuously. Thus, the size of a species pool (species richness) is indeterminate and unpredictable. The theory of species equilibrium, namely, that the steady-state number of species, found on an island or isolated patch of habitat due to a

balance between the immigration of new species and the extinction of old residents (MacArthur and Wilson 1967, Wilson 1992) is inadequate because it denies the reality of chance.

Heterogeneity and Non-saturation

The basic arguments of the currently dominant energy hypothesis are: (1) species richness is a measure of available energy, and (2) the product of a balance between immigration and extinction which causes richness to approach its theoretical maximum over time (MacArthur and Wilson 1967). Therefore, this hypothesis is that species richness in similar environments is the result of inevitable convergence. In general, tree species richness supports this and increases in direct relation to precipitation or AET, suggesting that a positive relationship exists between diversity and productivity of the habitat (Latham and Ricklefs 1992). But this is not always true. There are many examples of species richness decline at high habitat productivity levels (Ricklefs 1987, Latham and Ricklefs 1992). The total number and species of plants within a community may reflect total productivity, but species richness does not. Different species have different individual size, population and distribution patterns and thus have different energy needs and different ecological roles in an ecosystem. Some species, known as keystone species (Wilson 1992), affect the survival and abundance of many other species in the community in which they live. In contrast, the presence of some species may be caused by, and be largely dependent on, the existence of other species.

Clearly, species is not an energy or ecological unit. Theoretically, every species has a unique niche because every species has at least one physical or behavioral characteristic that defines it from other species (Solbrig 1991) even though the current measures of environmental parameters are too crude to distinguish all differences among species. The ecological inequality of species indicates that the number of species present is not a function of the physical environment. On the other hand, all regions exhibit heterogeneity and patchiness and no environment is completely homogeneous. This variability and patchiness in the environment provides a foundation for the coexistence of species. Consequently, competition seems less important as a determinant of species richness throughout a large scale biogeographic region than on a local site. However, species richness does not always tend toward its possible maximum largely due to the effect of chance. There is reason to assume that nowhere in the world have resources been fully utilized by plants. A measure of energy availability cannot even allow prediction of the maximum number of species in a region because plants have the ability to expand local environmental constraints during colonization. If species saturated biological communities exist within limits set by local conditions, new species could not join the community without the compensating disappearance of others

(Ricklefs 1987). But many successful introductions of exotic species cannot be shown to have caused an apparent loss of native species. In subtropical eastern Asia, for example, where tree species richness is about four times that of subtropical eastern North America, about 50 species of trees and woody vines introduced from eastern North America have successfully colonized without the compensating disappearance of the native species. American *Robinia pseudoacacia* L., *Campsis radicans* Seem., *Sabina virginiana* (L.) Antoine, *Pinus elliottii* Engelm., *P. taeda* L., *P. rigida* Mill., *Magnolia grandiflora* L., *Carya illinoensis* (Wangenh.) Koch, and *Liriodendron tulipifera* L., all now grow well in China and do even better locally than their eastern Asian species pairs. Of them, *Robinia pseudoacacia* and *Campsis radicans* have escaped from plantations and gardens and became naturalized species in China (He and Gu 1990). In these cases, competition between exotic and native species has led to increased diversity rather than extinction and loss of species in the area. Thus, a climate or energy hypothesis alone cannot explain this fact of additional species richness because both neglect historical plant evolution and migration.

Previous studies have usually concentrated on a small taxonomic group of organisms and thus failed to provide a general theory for the existence of species pools. In short, what is present on a given site at a given time, or interval of time, is a product of chance. The natural processes flowing in a river of information are relatively deterministic, but the residents on site at a given time are only those who then happen to reside there.

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